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Recurrent selection for groat-oil content in oats

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Recurrent selection for groat-oil content in oats

by

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GENERAL INTRODUCTION

Oats (Avena sativa L.) generally is regarded as one of the world's more nutritious cereal grains. Oat protein equals or surpasses that of the other cereals both in quality and quantity (Peterson and Brinegar, 1986). Additionally, oats has the highest groat (caryopsis) oil content of the temperate cereals (Weber, 1973; Price and Parsons, 1975) and, hence, the highest gross energy value. Oat oil is of superior quality, being relatively low in linolenic and high in linoleic acid (Kalbasi-Ashtari and Hammond, 1977; Price and Parsons, 1975). Although high in gross energy value when fed to livestock, oats has a low net metabolizable energy content due to its high crude fiber percentage (Welch, 1986). As a result, the feed conversion efficiency is lower for oats than other feed grains and, hence, a greater amount of oats needs to be fed to achieve equivalent live-weight gains. The failure of oats to compete economically with other feed grains has led to declining production. Oat production in the United States has fallen from a recent peak of 10.9 million metric tons in 1975 to 6.8 million metric tons in 1984 (Schrickel, 1986).

Recently, low commodity prices for maize (Zea mays L.) and soybeans (Glycine max (L.) Merr.), and concern about crop rotation and soil conservation practices have led to an increasing interest in crop diversification in midwestern USA agriculture. While new crop species are possible options to consider for diversification, expanded production of minor crops should not be overlooked. Preexisting adapted germplasm of crops such as oats offers potential for rapid development of unique cultivars.

Market expansion for oats could occur through breeding cultivars suited not only as a feed grain but also for novel culinary and industrial uses. Returning oats to profitability could result in increased production and, hence, greater crop diversity.

An increase in groat-oil content could lead to greater energy value for oat grain (Stothers, 1977), and the possibility for oats to be used as a source of edible vegetable oil (Frey and Hammond, 1975) and natural antioxidant compounds (Hammond, 1983). In the past, oats has not been used as an oilseed source because of its low caryopsis oil content and the presence of lipase which hydrolyzes the oil (Frey et al., 1975). Evidence is accumulating, however, which suggests that increasing the groat-oil content of oats is possible. Brown and Craddock (1972) reported that groat-oil content ranged from 3.1 to 11.6% for 4500 entries in the USDA world oat collection. Progeny mean heritabilities for groat-oil range from 68 to 93% (Baker and McKenzie, 1972), and single plant heritabilities have been reported as high as 83 to 98% (Stuke, 1960) and 59 to 79% (Brown et al., 1974). Groat-oil content is inherited polygenically (Brown et al., 1974; Frey et al., 1975) and gene action is primarily additive (Baker and McKenzie, 1972; Brown et al., 1974; Thro and Frey, 1985). Environmental modification of groat-oil content is minor relative to genetic effects (Frey and Hammond, 1975; Thro and Frey, 1984).

The value of introgressing wild oat germplasm into the cultivated oat gene pool for improving traits of economic importance has been well documented (Lawrence and Frey, 1975; Takeda and Frey, 1976; Cox and Frey, 1985; Frey, 1986). Recently, Thro and Frey (1985) have demonstrated

that high oil alleles from cultivated oats and the hexaploid wild oat A. sterilis L. are complementary. The range of groat-oil content for A. sterilis is similar to that of cultivated oats (Brown and Craddock, 1972; Rezai, 1977), but since the alleles from the two species are complementary, it should be possible to combine them into a single genotype with greatly increased groat-oil content.

Phenotypic recurrent selection is a population breeding procedure well suited to traits with high heritability (Allard, 1960). Selected individuals are chosen solely on their phenotypic merit and recombined to form an improved population. Increases in seed oil content have been reported in both maize (Sprague et al., 1952) and soybeans (Burton and Brim, 1981; Burton et al., 1983) by using some form of phenotypic selection.

The specific objectives of this research were to:

1. Use high-oil alleles from both A. sativa and A. sterilis to develop a population of oats adapted to the midwestern USA and suitable for phenotypic recurrent selection for high groat-oil content;
2. Evaluate the effectiveness of phenotypic recurrent selection as a breeding method for increasing groat-oil content of oats;
3. Determine the genetic gains in groat-oil content that can be expected per cycle of phenotypic recurrent selection; and
4. Identify correlated changes which may occur in unselected agronomic traits when groat-oil content is selected.

LITERATURE REVIEW

Oats as an Oilseed Crop

According to Hammond (1983), Dubovitz suggested in 1918 that oats might be used as a source of edible vegetable oil. Dubovitz calculated that oats with 7.17% groat-oil would yield enough oil to offset the cost of the grain plus the solvent extraction. More recently, Frey and Hammond (1975) estimated a groat-oil content of 17% would be required for oats to give a return equal to maize and soybeans in the midwestern USA. Currently, oil content of commercial oat cultivars averages approximately 4-6% (Frey and Hammond, 1975). Mattsson (1985) reported groat-oil content for Swedish cultivars to range from 3.9 to 8.8% whereas Welch (1975) found that British cultivars averaged 5%.

To a large extent, interest in oat oil is due to its superior fatty acid composition. Frey and Hammond (1975) analyzed 64 oat genotypes from several Avena species and found the major fatty acids of the oil were palmitic (18.9%), stearic (1.7%), oleic (42.2%), linoleic (35.5%), and linolenic (1.8%). Small amounts (<0.1%) of lauric, myristic, palmitoleic, and arachidic acids also were detected. Similar fatty acid profiles of oat oil have been reported by other researchers (Price and Parsons, 1975; Youngs and Puskulca, 1976; de la Roche et al., 1977; Sahasrabudhe, 1979; Mattsson, 1985). Welch (1975) found higher linoleic acid content in oat oil than reported by others, but his data were collected on greenhouse-grown materials. The variation in fatty acids except stearic was considerable. Most samples had less than 2% linolenic

acid. High linolenic acid content is undesirable because it oxidizes so readily, and it may also act as a catalyst in the oxidation of other fatty acids, particularly linoleic acid (Smouse and Chang, 1967). Fatty acid oxidation is believed to be the major cause of rancidity in soybean oil (Ho et al., 1978).

Oat flour extracts sometimes have unique antioxidant properties (Peters and Musher, 1937), and the compounds responsible for antioxidant activity occur in the lipid fraction (Caldwell and Pomeranz, 1973). Such compounds are glyceryl esters of hydroxycinnamic, ferulic, and caffeic acids (Daniels et al., 1963; Daniels and Martin, 1964, 1968) and the fat soluble tocopherols (vitamin E). The α form is the major tocopherol found in oat oil, but β- and γ-tocopherols have been detected in minor amounts (Kalbasi-Ashtari and Hammond, 1977).

The disadvantages of oats as a source of edible vegetable oil have been listed by Hammond (1983): (a) the low oil contents in current cultivars, (b) high and low oil tissues of the oat grain are difficult to separate, and (c) oat grain contains lipase which causes rancidity. Stuke (1961) has shown that the embryo of oat grain is oil rich, and Youngs et al. (1977) have suggested that both the scutellum and embryo axis were high in lipids. Of the total grain lipids, Beringer (1966) found 30.7% in the embryo axis, while Price and Parsons (1979) reported 21.2%.

Lipid-related enzymes cause rancidity problems for oat processors (Youngs, 1986). The hydrolytic enzyme lipase produces free fatty acids from triglycerides and partial glycerides. Lipase occurs on the surface

of the caryopsis (Hutchinson et al., 1951; Martin and Peers, 1953) and perhaps in the aleurone layer (Youngs, 1986). Various ways for reducing lipase have been investigated (Hutchinson et al., 1951; Moran, 1952; Frey and Hammond, 1975; Youngs, 1978); for example, (a) boiling the caryopses in water followed by vacuum drying, (b) grinding caryopses in ethanol and extracting with heptane, and (c) breeding genotypes with low lipase activity. Frey and Hammond (1975) screened 352 oat cultivars for lipase activity and, although none had zero activity, considerable variation did exist.

Inheritance of Oil Content in Oats

The inheritance of groat-oil content in oats is polygenic with largely additive gene action. Brown et al. (1974) analyzed F_1 and F_2 populations derived from crosses among eight parents and found groat-oil contents of the F_2 segregates were approximately normally distributed and mean oil contents of the F_1 and F_2 populations were similar to the mid-parental values. General combining ability (gca) was more important than specific combining ability (sca). Broad-sense heritability for groat-oil content ranged from to 75 to 79%. Baker and McKenzie (1972) reported that (a) average oil contents of random F_4 lines from 12 oat matings approximated the midparental values, and (b) progeny mean heritability ranged from 68 to 93%. Gene action for groat-oil content was additive in studies of Karow and Forsberg (1984). Oil content in a Dal x Exeter mating was under additive genetic control, whereas a major dominant allele for high oil content was detected in a Sauk x Dal

mating. Broad-sense heritability estimates for oil content were 83% and 62% in these matings, respectively. In three oat matings, Thro and Frey (1985) found that additive genetic effects accounted for 95, 80, and 50% of the variation among generation means. No dominance effects were detected.

Genetic control of groat-oil content in interspecific Avena matings is similar to that reported for intraspecific matings. Frequency distributions for three A. sativa x A. sterilis matings presented by Frey et al. (1975) indicate polygenic control of oil content. Mean groat-oil content of the F_2-derived lines from each cross was higher than the corresponding midparental value which implied partial dominance for high oil. Additional studies by Frey and Hammond (1975) showed similar results. Elliott et al. (1985) reported studies showing significant gca for groat-oil content with no dominance, and additive gene action for oil content was found by Thro and Frey (1985). In 12 interspecific matings (A. sativa x A. sterilis), F_2 progeny means were similar to their respective midparental values.

Groat-oil content in oats is determined largely by the genotype of the maternal plant. Brown and Aryeetey (1973) report a strong maternal effect in reciprocal crosses among A. sativa cultivars, and Brown et al. (1974) and Karow and Forsberg (1984) found no differences in oil content between F_1 hybrids and F_2 populations derived from reciprocal A. sativa matings. In four interspecific (A. sativa x A. sterilis) matings, Elliott et al. (1985) found no consistent cytoplasmic effects for oil content.

Genotype x environment interaction is relatively minor for groat-oil content. Baker and McKenzie (1972) noted the absence of cultivar x year and cultivar x site interaction for groat-oil. In Iowa, Frey and Hammond (1975) found oil content of oats was subject to significant environmental effect, and Thro and Frey (1984) show variation associated with cultivars was greater than cultivar x location interaction.

Correlation of Groat-Oil Content with Other Traits

Oil is only one component of oat caryopses, with the groat being composed primarily of carbohydrates and protein. Changes in the level of one component should lead to correlated changes in the others. From a survey of biochemical pathways in plants and their energy requirements, Penning de Vries et al. (1974) concluded that, under aerobic conditions, 1 gram of glucose would be used to produce 0.83 grams of carbohydrate, 0.40 gram of protein, or 0.33 gram of lipids. Obviously, the glucose requirement for oil is much greater than for carbohydrate and somewhat greater than for protein. Thus, with a fixed rate of photosynthate production, it follows that increases in the oil content of a grain should reduce both protein percentage and yield. Mitra and Bhatia (1979) calculated the bioenergetic cost of increasing oil content in peanut (Arachis hypogaea L.) to be least when accompanied by a reduction in protein percentage. Increasing oil content at the cost of carbohydrate is bioenergetically the most expensive.

The relationship between oil and protein contents in oats tends to be negative although often nonsignificant. Brown et al. (1966) reported

significant correlations of -0.312 and -0.477 between oil and protein contents for spring and winter oats, respectively. Several cultivars, however, had high levels of both oil and protein. Forsberg et al. (1974) noted a nonsignificant negative relationship for a group of adapted oat cultivars, and for segregates from diploid x hexaploid matings, the correlation between oil and protein contents was positive and nonsignificant. An investigation by Youngs and Forsberg (1979) showed a negative relationship between oil and protein percentages for 7 of 16 midwestern environments, of which 3 were significant. Oil and protein had significant positive associations in two of the locations.

The correlation of groat-oil content and grain yield has been investigated by several authors. No association between the two traits was reported for spring oats by Brown et al. (1966), but Forsberg et al. (1974) and Thro and Frey (1984) found positive relationships for oil content and yield, some of which were significant. Gullord (1986) noted only one significant (negative) relationship between oil content and grain yield in 28 location-year combinations. No association apparently exists between oil content and kernel weight, kernel density, test weight, groat weight, or groat percentage (Brown et al., 1966; Baker and McKenzie, 1972; Brown and Craddock, 1972; Forsberg et al., 1974; Gullord, 1980).

Introgression of Wild Germplasm Into Adapted Gene Pools

The value of introgressing germplasm from wild and weedy relatives into domesticated gene pools has been demonstrated for several crop species (Stalker, 1980; Frey, 1983; Frey et al., 1984). Most early

attempts at introgression were confined to the transfer of oligogenic disease resistance from wild or weedy types to their cultivated counterparts (Clayton, 1947; Bremer, 1961; Ling et al., 1970). Successful introgression of genes controlling yield has occurred in maize, sugarcane (Saccharum officinarum L.) and tobacco (Nicotiana tabacum L.) following hybridization with wild relatives (Reeves, 1950; Panje, 1972; Matzinger and Wernsman, 1967). In oats, Lawrence and Frey (1975) found transgressive segregates 20% higher yielding than their cultivated recurrent parent for several interspecific matings. Studies by Takeda and Frey (1976) and Kuenzel and Frey (1985) have shown similar results for vegetative growth rate and protein percentage, respectively.

Recent studies suggest that wild oat germplasm also may be of value for improving the groat-oil content of cultivated oats. Frey and Hammond (1975) examined caryopsis oil contents in accessions of five diploid (A. brevis, A. ludoviciana, A. pilosa, A. strigosa, A. wiestei), one tetraploid (A. barbata), and three hexaploid (A. fatua, A. sativa, A. sterilis) oat species. Oil contents ranged from 3.5 to 9.0% for the diploids, 5.5 to 8.0% for the tetraploid, and 2.0 to 11.0% for the hexaploids. Oil content of A. sterilis ranged from 4.5 to 11.0%, and according to Frey and Hammond (1975), this species should be a useful source of alleles since it crosses readily with cultivated oats. Evidence that the high groat-oil alleles carried by A. sativa and A. sterilis are different and complementary was provided by Thro and Frey (1985). Transgressive segregates for oil content were noted in 12 interspecific matings between four A. sterilis accessions and three A. sativa

cultivars. Five of the 12 matings gave mainly low transgressive segregates while four gave mainly high transgressive segregates.

The question of how best to incorporate wild or exotic germplasm into cultivated gene pools requires attention. The procedure best suited for introgression of exotic germplasm allows for the greatest increase in genetic variation for a given trait while reducing the overall performance of a population least. Useful alleles from exotic germplasm will often be linked to, or associated with, other alleles that condition unadaptiveness to a new environment, so identification of useful alleles in an introgressed population will be dependent upon the percentage of exotic germplasm present and the degree of genetic recombination that takes place during introgression.

Introgression studies in autogamous species have centered around the use of two-way (adapted x exotic) and three-way [(adapted x exotic) x adapted] crosses. Two- and three-way crosses carry 50 and 25% exotic germplasm, respectively, with the three-way cross providing the greatest opportunity for recombination. Thorne and Fehr (1970) examined this issue with soybeans and found that mean yields and genetic variances of the two-way cross populations were significantly lower than those of the three-way cross populations. A greater proportion of superior lines were found in populations from three-way crosses. Similar studies by Khalaf et al. (1984) showed that progenies from three-way soybean crosses were more variable and agronomically superior to those of either two-way or four-way [(adapted x exotic) x (adapted x exotic)] crosses.

Based on line performances, Eaton et al. (1986) have suggested that

the three-way cross and first backcross are the preferred methods of introgressing exotic germplasm into wheat (Triticum aestivum L.). Although cross means differed little, the greatest number of high yielding lines were produced in three-way and first backcross populations.

In oats, Williams (1969) found three-way cross populations to be higher yielding on average than those for two-way crosses. Three-way cross means frequently were higher than expected. The restoration of favorable epistatic gene combinations from adapted parents and/or the breakup of linkages from unadapted germplasm were suggested as causes for three-way cross superiority.

Cyclical or population breeding procedures offer great opportunity for genetic recombination, and hence, are well suited for introgression of exotic germplasm into adapted gene pools. Difficulties in the artificial hybridization of self-pollinated crops have restricted the use of such methods to the allogamous species. Phenotypic recurrent selection has been effective for isolating introgressed lines of maize with acceptable ear height (Vera and Crane, 1970), days to silking (Troyer and Brown, 1972), and disease resistance (Genter, 1976). Mild selection pressure in introgressed populations allows for the breakup of unfavorable linkages (Compton et al., 1979).

Recurrent Selection in Autogamous Crops

Recurrent selection was conceived and originally utilized for genetic improvement of quantitative traits in allogamous crop species (East and Jones, 1918). During recurrent selection, frequencies of

favorable alleles are increased gradually through a cyclical procedure of (1) progeny development, (2) progeny evaluation, and (3) recombination of superior genotypes (Hallauer, 1985). Despite its theoretical advantages (Bailey and Comstock, 1976), recurrent selection has not been used extensively in the self-fertilizing species. Difficulty in getting adequate numbers of crossed seeds has limited its use.

Development of better crossing techniques should allow for greater use of recurrent selection with autogamous species. Application of genetic male sterility to facilitate hybridization in soybeans has been proposed by Brim and Stuber (1973). Sorrels and Fritz (1982) have outlined recurrent selection procedures applicable to wheat and cotton (Gossypium hirsutum L.) based on dominant male-sterile alleles. Enhanced hybridization of cereal crops via approach crossing has been demonstrated by Curtis and Cray (1958) and McDaniel et al. (1967).

Incorporation of early generation testing into recurrent selection schemes for autogamous crops allows rapid cycling. Fehr and Ortiz (1975) have shown a theoretical advantage of S_1 line testing for recurrent selection in soybeans. Empirical data support the use of replicated S_1 line testing in recurrent selection for soybeans for grain yield (Kenworthy and Brim, 1979), protein percent (Brim and Burton, 1979; Miller and Fehr, 1979), iron deficiency chlorosis (Prohaska and Fehr, 1981), and phytophthora root rot (Walker and Schmittenner, 1984). Significant yield increases for soybean via S_2 and S_3 line recurrent selection have been reported also (Sumarno and Fehr, 1982; Piper and Fehr, 1987).

Recurrent selection that encompasses early generation evaluation has been used in other autogamous crop species. Guok et al. (1986), who used recurrent selection for yield in peanuts with replicated S_1 line testing, obtained a 10% increase in fruit yield from two cycles. The highest yielding family from either the C_2 or C_3 populations was not significantly better than the best family of the C_1 population however.

Utilizing F_3 family selection, Byrne and Rasmusson (1974) practiced bidirectional selection for strontium content in wheat. Average responses per cycle were 7.4 and -12.4% for the high and low populations, respectively. After two cycles of F_3 progeny recurrent selection, McNeal et al. (1978) reported a 2.5% increase in protein content of wheat. In a similar study, Loffler et al. (1983) obtained gains of only 0.5% per cycle.

In oats, Payne et al. (1986) obtained a gain in grain yield of 11.5% over three cycles of F_4 line recurrent selection. Cycle time averaged four years, so a per annum gain was 0.95%. McFerson (1987) got increases in groat-protein yield of 13, 16, and 12% over three cycles in three oat populations subjected to S_1 line recurrent selection. Groat-protein yield of the best C_3 line was significantly higher than the best C_0 lines in each population.

Phenotypic Recurrent Selection

Progeny testing, although necessary when dealing with traits of low heritability, requires at least one extra generation to complete a cycle of recurrent selection. When dealing with traits of moderate to high

heritability, progeny testing offers no advantage. Satisfactory gains can often be made by selecting solely on individual phenotypic merit.

Phenotypic recurrent selection has been applied extensively to the genetic improvement of forage and pasture species. Successful phenotypic recurrent selection within each of two broad-based alfalfa (Medicago sativa L.) gene pools has been demonstrated for leafhopper tolerance, rust, leafspot, bacterial wilt, and anthracnose resistance (Hanson et al., (1972). In red clover (Trifolium pratense L.), phenotypic selection has been used to improve stem length (Bowley et al., 1984) and flower morphology (Taylor et al., 1985). Improved rust and purple leafspot resistance has been reported in orchardgrass (Dactylis glomerata L.) by Miller and Carlson (1982) and Zeiders et al. (1984), respectively. Burton (1974, 1982) has described a recurrent restricted phenotypic selection procedure by which forage yields of Pensacola bahiagrass (Paspalum notatum var. saurae Parodi) were significantly increased.

Response to phenotypic recurrent selection has been demonstrated for several traits in tobacco. Over four cycles of phenotypic or mass selection (with recombination), Matzinger and Wernsman (1968) observed a significant linear increase in the green weight of leaves. Index mass selection has been used to increase leaf number while reducing plant height, traits normally negatively correlated (Matzinger et al., 1977). Van Sanford and Matzinger (1983) increased seedling weight via phenotypic selection in both stress and nonstress environments. Total alkaloid content of burley tobacco has been reduced 23% in five cycles of phenotypic selection (Gupton, 1981). Beatson et al. (1984) practiced divergent mass

selection for carotenoid concentration and obtained average responses of 13 and 26% in high and low populations, respectively.

Application of phenotypic recurrent selection procedures to improve grain crops has also been reported. Burton and Brim (1981) via phenotypic selection in soybeans increased seed oil content by 0.35% per cycle. In a similar study, Burton et al. (1983) increased the oleic acid percentage of soybean oil 1.6% per cycle.

In cereals, Khadr and Frey (1965) used phenotypic recurrent selection to increase 100-seed weight of oats by 12% per cycle. Busch and Kofoid (1982) used recurrent selection to increase kernel weight of spring wheat by 3 and 7% per cycle. Avey et al. (1982) used phenotypic recurrent selection to obtain early heading in winter wheat. Greatest gains were made in the first cycle of selection.

Explanation of Dissertation Format

This dissertation contains two sections. Section I describes the use of phenotypic recurrent selection for high groat-oil content in an adapted introgressed population of oats. Section II investigates the correlated response to high oil section in unselected agronomic traits.

Each section is in the form of a complete manuscript that will be submitted for publication with little or no modification. References are cited in "Additional References Cited" following the General Conclusions. An appendix to the dissertation follows the Additional References Cited. The alternate format is authorized on page 6 of the 1985 edition of the Iowa State University Thesis Manual.

SECTION I. RECURRENT SELECTION FOR GROAT-OIL CONTENT IN OATS

ABSTRACT

An improvement in the groat (caryopsis) oil content of oats (Avena sativa L.) may lead to development of oilseed oat cultivars. Three cycles of phenotypic recurrent selection for high groat-oil content were conducted in an introgressed oat gene pool, constructed by combining high oil alleles from A. sativa with those of its wild relative, A. sterilis L. Selection for groat-oil content was applied to individual F_1 plants, recombining the highest 10% to form the improved populations. One year was required to complete each cycle of selection. Gain from selection was evaluated by field testing 100 random and 100 selected lines from the base (C_0) and each improved population (C_1, C_2, C_3).

Groat-oil content increased linearly 9.26 g kg^{-1} per cycle of selection, which resulted in a linear increase of oil yield equal to 21 kg ha^{-1} per cycle. The largest gain from selection was realized for both traits in the first selection cycle. Broad-sense heritability and genetic variance remained high and significant in all cycles which suggests continuing progress from additional cycles of recurrent selection. Realized heritability for groat-oil content was 0.68 ± 0.05. Of the 400 random lines evaluated, the top 10 lines for groat-oil content were from the C_3 population. Highest groat-oil content of any individual line was 144.8 g kg^{-1}. The fact that some high-oil oat lines were equivalent to check varieties for all agronomic traits measured suggests that selection for oil content had little effect on those traits. Results suggest that phenotypic recurrent selection and the introgression of

wild oat germplasm into the cultivated oat gene pool can be effective in the modification of chemical composition of the oat grain.

Additional index words: *Avena sativa* L., *Avena sterilis* L., oil yield, introgression, phenotypic recurrent selection, heritability, genetic variance.

INTRODUCTION

Oats (Avena sativa L.) has the highest groat (caryopsis) oil content of the temperate cereals (Price and Parsons, 1975). Increasing the groat-oil content of oats further could lead to improvements in feeding value of the grain (Stothers, 1977) and the potential for oats to be grown as a source of an edible vegetable oil (Frey and Hammond, 1975) and anti-oxidant compounds (Hammond, 1983).

Genetic improvement in the oil content of oats may be possible. It is inherited polygenically (Frey et al., 1975) with primarily additive gene action (Brown et al., 1974) and its heritability is high (Baker and McKenzie, 1972). Genetic variation for oil content exists both within cultivated oats (Brown and Craddock, 1972) and wild and weedy relatives (Frey and Hammond, 1975). Recently, Thro and Frey (1985) demonstrated the complementary nature of high-oil alleles found in the cultivated oat and its hexaploid progenitor A. sterilis L. Although the range of groat-oil contents found within A. sterilis is no higher than for cultivated oats (Rezai, 1977), it is expected that by combining alleles from the two species into a single genotype, groat-oil content would be greatly enhanced.

Phenotypic recurrent selection is a breeding procedure well suited to genetically modifying quantitatively inherited traits with high heritability. Despite its theoretical advantages (Bailey and Comstock, 1976), recurrent selection has not been used extensively in the self-fertilizing species. Difficulties have arisen in obtaining enough hybrid

seeds from crossing among selected lines and in producing adequate seed lots of progenies for testing. A recurrent selection schedule for spring cereals has been developed at Iowa State University which alleviates these problems and allows greater use of this method for oat breeding (Frey et al., 1988).

The objective of this study was to determine the response of groat-oil content and also oil yield per unit area from three cycles of phenotypic recurrent selection for groat-oil content in a nobelized oat population with high oil alleles from both A. sativa and A. sterilis.

MATERIALS AND METHODS

Gene Pool Development

The base population for this study was an oat gene pool systematically constructed by combining alleles for high groat-oil content from A. sativa and A. sterilis and good agronomic performance from locally adapted cultivars. Development of the gene pool was begun previously and partially described by Thro and Frey (1985). Briefly, eight interspecific biparental matings were made by crossing, at random, each one of eight high-oil A. sativa cultivars with a different high-oil A. sterilis accession (Table 1). Parents of both species were chosen for high groat-oil content regardless of their adaptation to the target area of cultivation. Three-way or first species backcrosses were then formed by mating, at random, interspecific F_1 plants to a group of locally adapted cultivars (agronomic group I in Table 1).

A flow chart for development of the gene pool is presented in Figure 1. Seed from each three-way mating was advanced to F_2 and ca. 8000 seeds were space sown in the field (1 seed per 15 cm row, 0.9 m between rows) at the Agronomy Field Research Center near Ames, Iowa. Plants were culled during the growing season for acceptable maturity and height and 4447 were harvested individually. Following culling for trueness to an A. sativa seed type (lack of pubescense, pigment, and awns), enough seed from the 667 remaining lines was dehulled to give 3.5 to 5.0 g of oven-dried groats. These were evaluated for oil content using the nuclear

Table 1. Geographic origin and groat-oil content of parents used to develop an adapted high-oil oat gene pool

Parent	Origin	Groat-oil g kg^{-1}
	A. sterilis	
PI 282731	Israel	91[a]
PI 296247	Israel	97
PI 309193	Israel	100
PI 309430	Israel	91
PI 324806	Algeria	93
PI 411540	Algeria	102
PI 411971	Iraq	94
PI 412443	Sicily	97
	A. sativa: High-oil group	
CI6857	FL, USA	107
Lodi	WI, USA	82
MO05499	MC, USA	92
Wright	WI, USA	86
MO0205	MO, USA	89
Orbit	NY, USA	72
CI3445	India	110
Dal	WI, USA	85
	A. sativa: Agronomic group I	
Noble	IN, USA	68
Otee	WI, USA	73
Spear	SD, USA	88
Lang	IL, USA	70
Stout	IN, USA	59
CI9273	IA, USA	93
Pettis	MO, USA	90
Y22-15-9	IA, USA	93
	A. sativa: Agronomic group II	
MO06195	MO, USA	67
IL75-1056	IL, USA	77
IL75-5743	IL, USA	69
NYA-11	NY, USA	93
D226-30-3-3	IA, USA	48

[a]According to Rezai (1977).

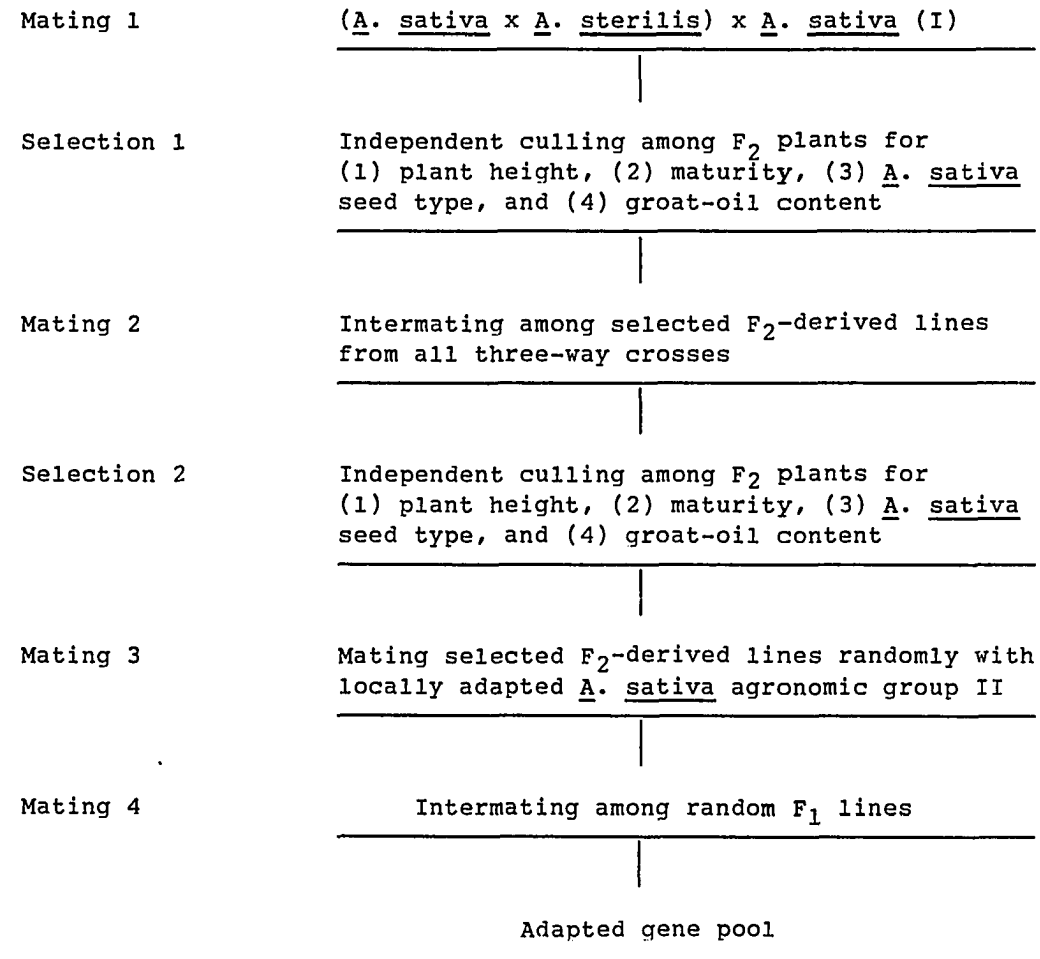

Figure 1. Flow chart for development of an oat gene pool with high-oil alleles from both A. sativa and A. sterilis

magnetic resonance (NMR) method[1] described by Conway and Earle (1967). Seventy-two F_2-derived lines, which included progenies from all three-way crosses, with groat-oil content of 75 g kg^{-1} or greater were selected and intermated, such that each mating involved parental lines derived from different three-way crosses. These intermatings were then advanced to F_2.

Approximately 2500 F_2 seeds were space sown in the field as described previously to begin a second cycle of culling. Independent culling for maturity, plant height, and an A. sativa seed type together with severe drought conditions resulted in only 286 harvested plants having sufficient seed for NMR oil analysis. Ninety F_2-derived lines with groat-oil contents of 95 g kg^{-1} or greater were selected from among the harvested plants.

Second species backcrosses were formed by mating[2] the 90 F_2-derived lines with a second group of locally adapted cultivars (agronomic group II in Table 1). Each F_2-derived line arising from the same cross was mated to a different cultivar. Backcross progenies were intermated at random with each line, on average, being mated to three others. Progeny from these matings sown in the field in 1983 were used as the base (C_0) population for this study.

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[1]Appreciation is expressed to Dr. D. E. Alexander and Ms. Evelyn Marriott, Agronomy Department, University of Illinois, Urbana, IL, who conducted all NMR oil analyses reported in this study.

[2]Appreciation is expressed to H. F. Rattunde, Agronomy Department, Iowa State University, Ames, IA, who made the second species backcrosses and intermated their progeny.

Recurrent Selection Procedure

In the spring of each year, selection cycles were initiated by space sowing approximately 3000-4000 F_1 plants. Plants were sown in rows, 90 cm apart and plants were spaced 15 cm apart within rows. All plants were grown at the Agronomy Field Research Center near Ames, Iowa. Experimental areas received a broadcast application of 34-22-28 kg ha^{-1} of N, P, and K, respectively, prior to planting. Starting at emergence, plants were sprayed at weekly intervals with an insecticide (Malathion) to control the spread of aphids that transmit the barley yellow dwarf virus.

During the growing season, independent culling was practiced on spaced oat plants for medium to short height, early maturity, lodging resistance, and A. sativa seed and panicle types. Following selection, ca. 1000 plants remained for harvest and groat-oil determination. Wide line nuclear magnetic resonance was used to analyze groats for oil content. Analyses were performed on seed samples from individual plants, dehulled to provide 3.5 to 5.0 g of oven-dried groats. Based on groat-oil content, the highest 10% of plants was chosen from each cycle to recombine. Selection of sib plants was avoided where possible.

Mating among progenies of selected plants was done each fall in the greenhouse. Matings were made at random by using the approach method (Curtis and Cray, 1958; McDaniel et al., 1967). Between 30 to 40 crosses were made per day, with eight to ten F_1 seeds obtained per cross. On average, each F_1-derived line was mated to four others, with care being taken to avoid assortative mating due to time of maturity and plant

height. Four to six F_2 plants per F_1-derived line were used for recombination. F_1 seeds for the intermating were mature by December of each year.

Evaluation of Response to Selection

Response to phenotypic recurrent selection for groat-oil content of oats was evaluated in a replicated experiment that contained lines from the base population and all selection cycles (i.e., C_0, C_1, C_2, and C_3). The evaluation experiment contained (a) 100 random F_1-derived lines from each of the C_0, C_1, C_2, and C_3, (b) 100 selected lines that were used to construct each of the C_1, C_2, and C_3, (c) four check varieties ('Starter', 'Webster', 'Ogle', and 'Noble') each entered five times per replication, and (d) the A. sativa and A. sterilis parents used to develop the C_0 gene pool. The experiment contained 726 entries. Selected and random lines from C_0 through C_2 were F_1-derived in F_3, whereas random lines from C_3 were F_1-derived in F_2. The evaluation experiment was conducted in a randomized complete block design with two replications in each of three locations: Ames, Kanawha, and Sutherland, Iowa. Nitrogen, phosphorus, and potassium were applied at rates of 34-22-28 kg ha^{-1} at Ames, 52-3-4 kg ha^{-1} at Kanawha, and 17-29-18 kg ha^{-1} at Sutherland prior to sowing. A plot was a hill (Frey, 1965) sown with 20 seeds and hills were spaced 30.5 cm apart in perpendicular directions. Two rows of hills were sown around the experiment to reduce border effects. Plots were sprayed with a systemic fungicide (Bayleton) to control leaf diseases. Traits measured or calculated were:

1. Days to heading (HD) - days from seeding to 50% of plants with full panicle emergence;
2. Plant height (HT) - distance (cm) from ground level to panicle tips;
3. Biomass (BM) - dry weight of the bundle of culms, expressed in Mg ha^{-1};
4. Grain yield (GY) - dry weight of threshed grain, expressed in Mg ha^{-1}; and
5. Harvest index (HI) - grain yield divided by biomass, expressed as a percentage.

Next, the two replications of an entry at a location were bulked. Bulking entry replications was necessary to provide sufficient seed for analysis and to keep evaluation costs minimal. This provided three bulked seed lots for each entry which were used for measurements of the following traits:

6. Test weight (TW) - weight of a standard volume of seed, expressed in kg m^{-3};
7. Seed weight (SW) - weight (g) of 100 random seeds;
8. Groat fraction (GF) - groat weight as a fraction of seed weight (a one-gram sample of seeds were manually dehulled) expressed in g kg^{-1};
9. Groat-yield (GTY) - product of grain yield and groat fraction, expressed in Mg ha^{-1};
10. Groat-oil content (GO) - enough seeds were dehulled to give 3.5 to 5.0 g of oven-dried groats which were evaluated using the

nuclear magnetic resonance method, expressed in g kg^{-1}; and

11. Oil yield (OLY) - product of groat yield and groat-oil content, expressed in Mg ha^{-1}.

Grain yield, biomass, and harvest index data were recorded for both replications at each location. Heading date and plant height were recorded for both replications at Ames and Kanawha, respectively.

Statistical Analyses

An analysis of variance was performed for each trait using standard statistical procedures (Cochran and Cox, 1957), with cycles as fixed and environment and lines within cycles as random effects. Quasi F-tests (Satterthwaite, 1946) were used to test for cycle main effects. Fisher's protected L.S.D. test was used to compare cycle means (Steel and Torrie, 1980). Replicated check varieties in each experiment provided an estimate of experimental error for those traits measured on replication bulks.

Realized heritability was estimated by regression of response on cumulative selection differential (Falconer, 1981), and the variance for the realized heritability estimate was calculated according to Hill (1972). Phenotypic (σ_p^2) and genotypic (σ_g^2) variances were estimated for each cycle of selection from the analyses of variance, and broad sense heritability was estimated as:

$$h^2 = \sigma_g^2 / \sigma_p^2$$

Standard errors of variance components and broad sense heritability were calculated by using the methods of Anderson and Bancroft (1952) and Dickerson (1969), respectively.

Linear regression of cycle mean on cycle number was used to determine realized gain per cycle of selection.

RESULTS AND DISCUSSION

Population Performance

Analyses of variance for the random and selected lines from C_0 through C_3 showed that cycle means differed significantly ($P < 0.01$) for groat-oil content and oil yield (analyses of variance not shown). Groat-oil content was increased 33% over three cycles of phenotypic recurrent selection (Table 2), an increase equivalent to 11% either per cycle or per year. The mean groat-oil content for C_3 represents an increase of 71% over the mean of the A. sativa parents used in constructing the C_0 gene pool and 135% over the mean of currently used commercial oat cultivars. Because the seed did not germinate, oil evaluations on the original A. sterilis parents could not be made. Gains made in groat-oil content were reflected in sizable increases in oil yield. Mean oil yield for C_3 was increased 33, 85, and 140% over the means of the C_0, the original A. sativa parents, and current commercial cultivars, respectively.

Interaction of cycles of selection with locations, although statistically significant ($P < 0.01$) for both groat-oil content and oil yield, was considered of minor importance because mean squares for the interaction were small relative to those for cycles. Partitioning of the interaction sum of squares showed that linear, quadratic, and residual components all were significant ($P < 0.01$) for oil yield, but only the linear component was significant ($P < 0.01$) for groat-oil content. Regressions of cycle means on cycle numbers in each location were all linear and positive but the slopes were heterogeneous which suggests

Table 2. Groat-oil content and oil yield for random C_0, C_1, C_2, C_3 lines, A. sativa parents, and check varieties averaged over three locations

Cycle	Groat-oil	Oil yield
	g kg^{-1}	Mg ha^{-1}
C_0	84.96	0.18
C_1	98.63	0.21
C_2	106.25	0.23
C_3	113.30	0.24
FLSD (0.05)[a]	3.16	0.02
A. sativa parents	66.44	0.13
LSD (0.05)[b]	2.57	0.02
Check varieties	48.16	0.10
LSD (0.05)[c]	2.51	0.02

[a]Applicable to cycle mean comparisons.

[b]Applicable to comparison of cycle means and A. sativa parents.

[c]Applicable to comparison of cycle means and check varieties.

that the location by cycle of selection interaction was due to differences in magnitude between cycles rather than differences in ranking among cycles. Thus, for purposes of presentation, mean response to selection over locations is used. Groat-oil content increased linearly 9.26 g kg^{-1} per cycle of selection (Figure 2), with the largest increase of 13.67 g kg^{-1} occurring in the first cycle. Thro and Frey (1985) reported a similar gain in groat-oil content from a single cycle of recurrent selection. Smaller, but significant, gains occurred in each of the two subsequent cycles. Selection for groat-oil content caused a concomitant linear increase of 21 kg ha^{-1} for oil yield (Figure 3). As with groat-oil content, the largest increase in oil yield occurred in the first cycle of selection; however, the gain in the third cycle was not significant.

The genetic variance for groat-oil content was reduced approximately 30% over three cycles of selection (Table 3). This reduction raises a question about the prospects for continued increases in groat-oil content from selection; however, the C_3 variance for this trait is primarily genetic in origin as shown by the high broad-sense heritability estimate. Thus, the likelihood of continued progress from recurrent selection for groat-oil content is good. Heritability estimates obtained in this study are higher than those previously reported for groat-oil content (Brown et al., 1974) which may be a manifestation of the introgressed alleles in this population. Probably nonadditive genetic effects did not bias heritability estimates upward because genetic variation for groat-oil content is largely additive (Thro and Frey, 1985). From a plant breeder's perspective, realized heritability is probably a more

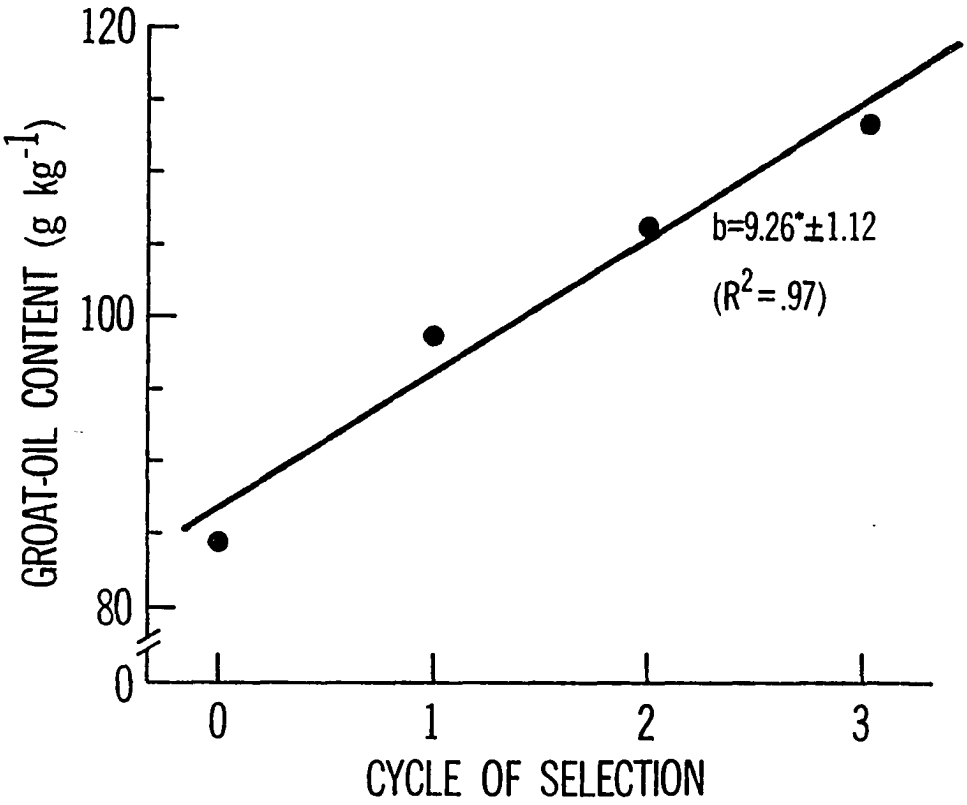

Figure 2. Response of an oat population to recurrent selection for groat-oil content

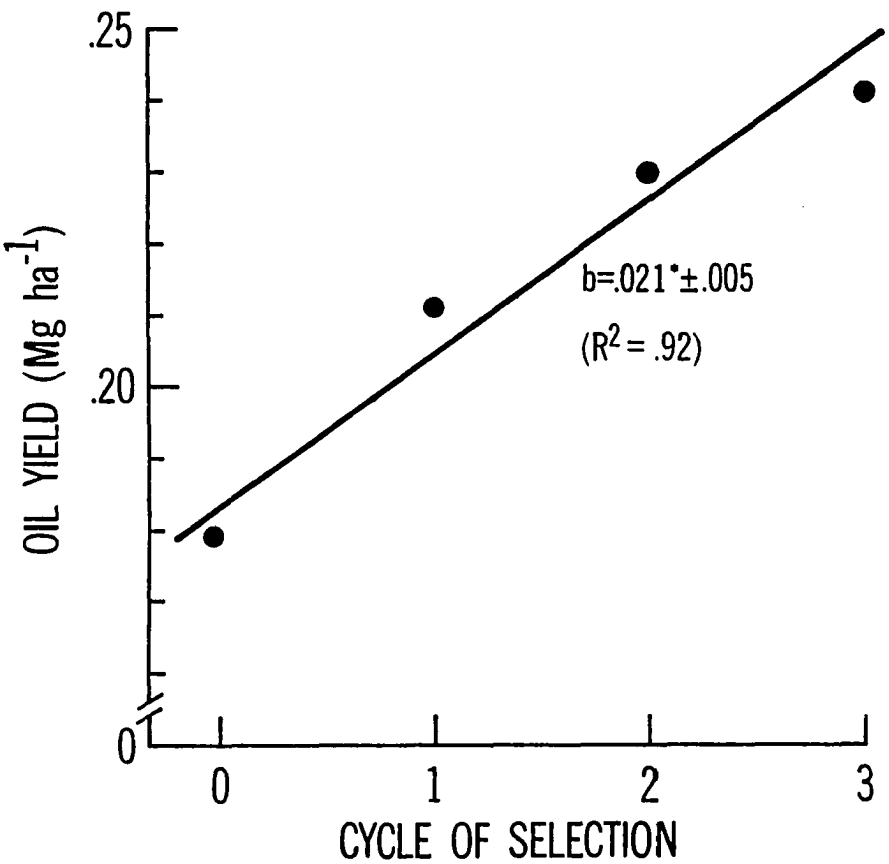

Figure 3. Increase of oil yield in an oat population subjected to recurrent selection for groat-oil content

Table 3. Broad-sense heritabilities (h^2) and genetic variances (σ_g^2) for groat-oil content and oil yield estimated from random oat lines from the base population and three cycles of recurrent selection when tested at three locations in 1986

Cycle	Groat-oil		Oil yield	
	h^2 ± S.E.	σ_g^2 ± S.E.	h^2 ± S.E.	σ_g^2 ± S.E.
				(x 10^{-6})
C_0	93.5 ± 14.1	109.54 ± 16.51	66.1 ± 14.5	853 ± 187
C_1	91.3 ± 14.7	95.05 ± 14.68	59.0 ± 14.7	720 ± 179
C_2	89.6 ± 14.1	78.29 ± 12.33	71.7 ± 14.4	1390 ± 278
C_3	88.3 ± 14.1	76.51 ± 12.33	69.4 ± 14.4	1203 ± 250

meaningful expression of what a plant breeder can accomplish than is heritability derived from variance components. In this study, realized heritability for groat-oil content was 0.68 ± 0.05.

Genetic variance and broad-sense heritability estimates for oil yield showed no consistent change with selection for groat-oil content. As for groat-oil content, the variance for oil yield was mainly genetic in origin.

Line Performance

Recurrent selection is a breeding method that, in theory, should, in each generation, increase the population mean and produce individual lines with ever greater performance. The production of ever better lines is of particular importance in autogamous species where pure lines are

used as cultivars. Sumarno and Fehr (1982) and Guok et al. (1986) reported significant gains in mean yield from recurrent selection in soybeans (Glycine max (L.) Merr.) and peanuts (Arachis hypogaea L.), respectively, but in neither study was the best C_3 line higher yielding than the best C_0 line. McFerson (1987), however, working with oats, got significant increases in groat-protein yield in three populations. The best C_3 line was significantly higher than the best C_0 line in each population. Of the 400 random lines evaluated in this study, the top ten lines for groat-oil content were from the C_3 population, with their mean being 131.3 g kg^{-1}, averaged over three locations. The corresponding average of the ten top C_0 lines was 104.5 g kg^{-1}. No C_0 line equaled or surpassed any of the top ten C_3 lines. The highest individual line was from C_3 with groat-oil content of 144.8 g kg^{-1}. Among the top ten lines for oil yield, six came from the C_3, three from the C_2, and one from the C_1 population. Mean oil yield for the top 10% of lines from C_3 was 0.35 Mg ha^{-1} compared to 0.24 Mg ha^{-1} for the top 10% of C_0 lines. The frequency distributions for groat-oil content and oil yield of oat lines clearly demonstrate the population and line improvements for both traits accomplished in three cycles of recurrent selection (Figures 4 and 5).

The value of introgressing wild oat germplasm into the cultivated oat gene pool for improving traits of economic importance has been well documented (Lawrence and Frey, 1975; Takeda and Frey, 1976). While making substantial improvements in single traits, other traits of agronomic importance may show a deviation due to the introgression of genes from the

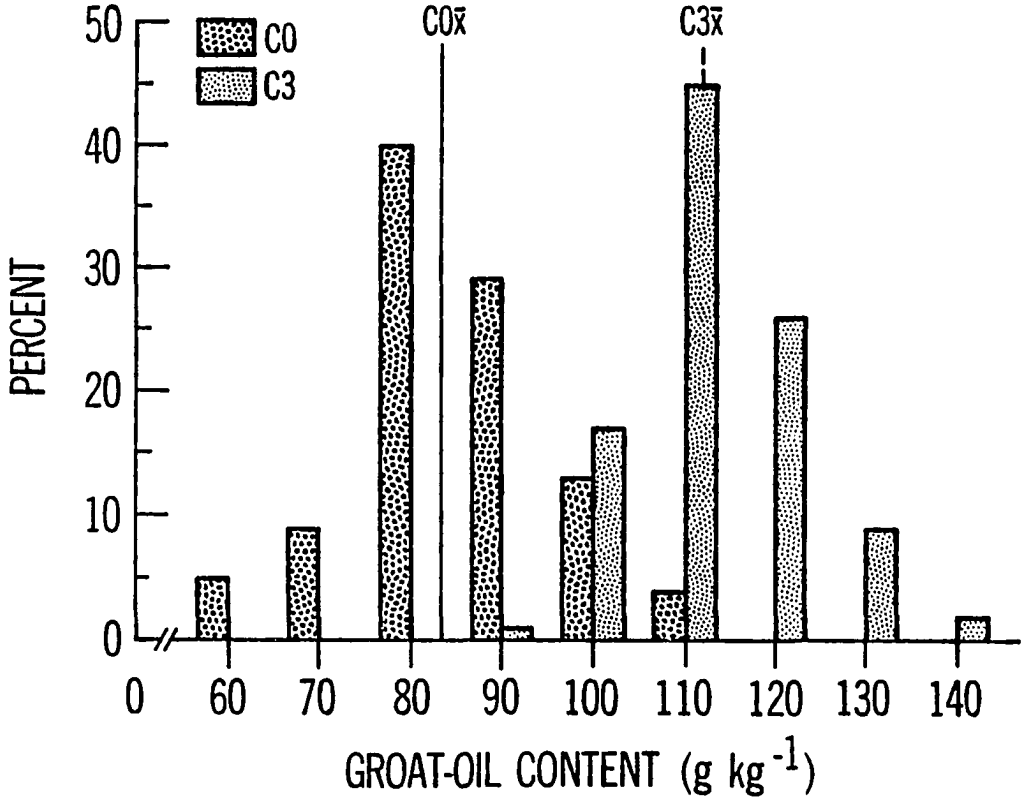

Figure 4. Frequency distributions for groat-oil contents of oat lines from the base population (C0) and third cycle of selection (C3) for this trait

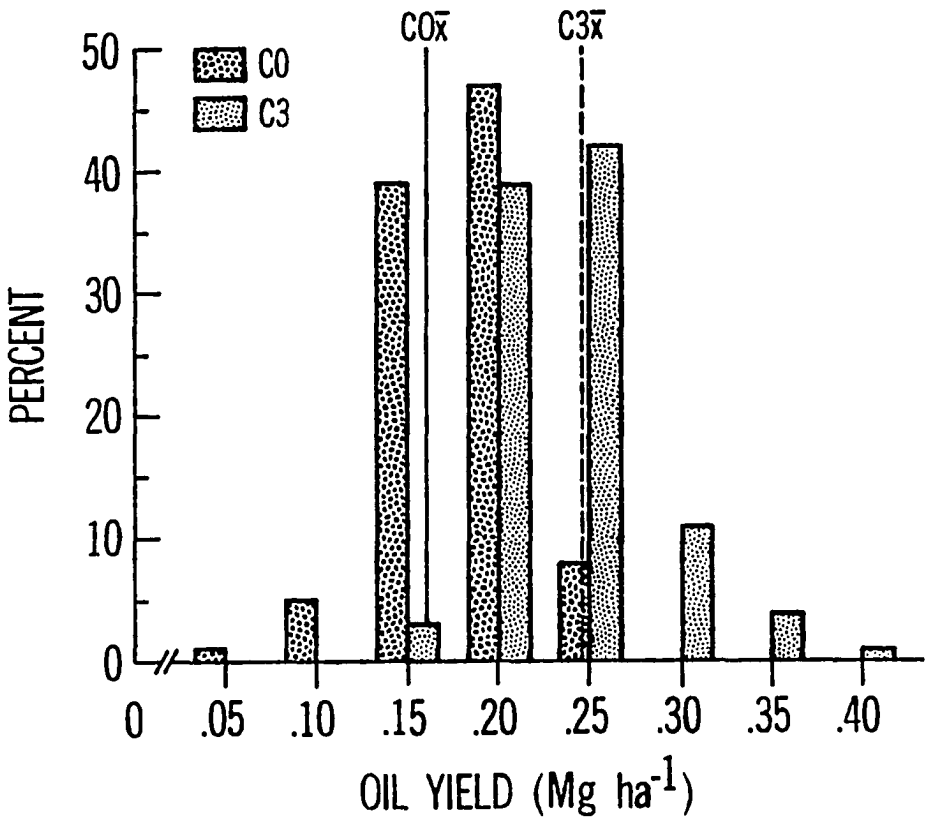

Figure 5. Frequency distributions for oil yield of oat lines from the base population (C0) and third cycle of selection (C3) for groat-oil content

donor genotypes that are deleterious to production and agronomic traits. Such genes may represent a random residue from the introgression or they may be linked to desired and, therefore, selected genes. With application of a correct breeding strategy, this type of deterioration need not occur. Careful selection of parents for the introgressed oat gene pool, crossing them in the correct order, and practicing mild selection for agronomic type resulted in a C_0 that was nobelized, well adapted to midwestern USA, and contained the diversity of high groat-oil alleles needed for rapid improvement of groat-oil content and oil yield. Agronomic profiles of the ten oat lines with the highest oil yield are presented in Table 4. Individual lines at least equal to the check varieties can be found for all traits measured. Several lines have a grain yield and biomass significantly higher than the check varieties, while all lines are equivalent for groat fraction and harvest index and superior for groat yield. Most lines have seed weight and test weight significantly lower than the check varieties however.

Phenotypic recurrent selection has proven to be an effective means of improving both groat-oil content and, indirectly, oil yield of oats. The success was to a certain extent dependent upon several factors unique to the crop, trait, and technique. The fact that groat-oil content of oats was determined by additive gene action, had high heritability, and was influenced little by environment made it possible to use early generation selection of individual plants at a single location. Further, oil analysis by NMR and use of the approach crossing procedure kept cycle time to a minimum. The introgression of high oil alleles from A.

Table 4. Means for agronomic traits of the 10 oat lines with highest oil yield and of check varieties tested in three locations in 1986

Line	Cycle	Trait										
		OLY	GO	GY	TW	GF	SW	GTY	BM	HI	HD	HT
		Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}	kg m^{-3}	g kg^{-1}	g	---Mg ha^{-1}--		%	days	cm
K734-18	3	0.41	130.3	4.45	393.69	713.1	2.52	3.17	10.30	43.2	81.0	90.5
K441-2	2	0.39	118.0	4.61	382.30	726.9	2.45	3.35	10.15	45.0	78.5	83.0
K361-4	2	0.35	117.4	4.36	354.70	695.3	2.37	3.05	9.90	44.3	80.5	79.5
K745-11	3	0.35	120.7	4.00	388.24	718.7	2.29	2.87	8.43	47.8	72.0	85.5
K693-9	3	0.33	128.2	3.60	392.91	717.2	3.02	2.59	7.73	46.5	75.5	94.5
K734-16	3	0.33	129.0	3.64	407.31	714.5	2.43	2.61	8.63	42.3	81.0	90.5
K726-3	3	0.33	111.7	4.20	374.25	687.3	2.50	2.89	9.42	44.8	79.0	88.5
J406-1	1	0.32	128.9	3.64	377.05	718.6	2.30	2.63	8.05	46.2	76.0	87.0
K801-15	3	0.32	128.0	3.50	382.40	714.2	2.72	2.50	7.85	44.4	81.5	93.5
K238-5	2	0.32	112.2	3.93	410.85	722.3	2.47	2.84	8.82	44.7	72.0	76.5
FLSD (0.05)[a]		0.06	8.3	0.80	33.25	54.0	0.30	0.60	1.68	5.4	1.6	8.2
Check varieties		0.10	48.2	3.08	415.55	711.6	2.98	2.02	7.03	44.1	77.5	82.7
LSD (0.05)[b]		0.05	5.2	0.58	24.09	39.1	0.22	0.43	1.22	3.9	1.1	6.0

[a]Applicable to line comparison.

[b]Applicable to comparison of lines and check varieties.

sterilis into the gene pool for recurrent selection insured genetic variation for this trait. Of course, only long-term recurrent selection studies will show the extent to which groat-oil content and oil yield of oats can be elevated. However, genotypes already recovered in the C_3 have groat-oil contents exceeding that previously reported for either A. sativa or A. sterilis by 35%. Frey and Hammond (1975) estimated an oat with 170 g kg^{-1} groat-oil content and current protein and yield levels could be grown economically as an oilseed crop. At the present rate of gain, two additional cycles of selection will be required to produce such an oat.

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SECTION II. CORRELATED RESPONSE TO RECURRENT SELECTION FOR GROAT-OIL CONTENT IN OATS

ABSTRACT

One hundred random oat (Avena sativa L.) lines from a base (C_0) and each of three populations (C_1, C_2, and C_3) improved for groat (caryopsis) oil content by phenotypic recurrent selection were evaluated for correlated changes in several unselected agronomic traits. In addition, the parents of the base population and four check varieties were evaluated for the same traits. Phenotypic recurrent selection for high groat-oil content resulted in no significant correlated response in mean expression of any trait. Mean grain yield, biomass, groat yield and harvest index of the improved populations were equal or superior to the mean of the parents and, with the exception of harvest index, equivalent to the mean of the check varieties. Mean test weight and seed weight of all populations were lower than for parents or check varieties. Selection for high groat-oil content caused a decline in genetic variance for test weight and groat fraction, but reductions in genetic variance for heading date and plant height may have resulted from culling for good agronomic type. Broad-sense heritability remained moderate to high for all traits except groat fraction. Phenotypic and genetic correlation coefficients revealed negative, though mostly nonsignificant, relationships between groat-oil content and several traits which may reflect a purported bioenergetic limitation to increasing groat-oil content in oats. Oil yield, however, was positively correlated with grain and groat yield, groat fraction, biomass and harvest index. Results suggest that

development of high-oil oat cultivars with current levels of production traits via phenotypic recurrent selection is possible.

Additional index words: *Avena sativa* L., *Avena sterilis* L., introgression, phenotypic recurrent selection, oil yield, correlated response.

INTRODUCTION

Oats (Avena sativa L.), although a nutritious feed grain, has a low net metabolizable energy content due to its high crude fiber percentage (Welch, 1986). Selection for high groat (caryopsis) oil content could improve not only feeding value of the grain (Stothers, 1977), but also facilitate novel culinary and industrial uses for the crop (Frey and Hammond, 1975). Oat oil, once extracted from the grain, is potentially a valuable edible vegetable oil because it is highly unsaturated and low in linolenic acid concentration (Youngs and Puskulca, 1976). Rapid oxidation of linolenic acid results in a flavor reversion and production of off-flavor components (Ho et al., 1978). Additionally, oat oil may also be of value as a source from which to extract compounds with antioxidant activity (Hammond, 1983).

Recent studies have demonstrated the possibility of increasing groat-oil content of oats through selection. Thro and Frey (1985) reported one cycle of phenotypic recurrent selection resulted in a genetic gain of 1.7% to 2.1% in groat-oil content. Selection was based on single plant progenies of three-way matings between A. sativa and its hexaploid progenitor A. sterilis L., thereby incorporating into single genotypes complementary high-oil alleles of both species. Continuing phenotypic recurrent selection within this gene pool, Branson (1987) obtained an average per cycle response of 9.26 g kg^{-1} (0.93%) and 21 kg ha^{-1} for groat-oil content and oil yield, respectively. Groat-oil content of some improved lines represented a threefold increase over that

presently available in oat cultivars.

Correlated changes in expression, either favorable or unfavorable, can occur between selected and unselected traits when genes conditioning both are pleiotrophic or linked. Genetic relationships between groat-oil content of oats and other chemical and production associated traits are not well understood. It is known, however, that groat-oil content is often positively correlated with grain yield (Thro and Frey, 1984) and sometimes negatively correlated with protein percentage (Youngs and Forsberg, 1979). No correlation apparently exists between groat-oil content and kernel weight, kernel density, test weight, or groat percentage (Brown et al., 1966; Baker and McKenzie, 1972; Brown and Craddock, 1972; Forsberg et al., 1974).

The purpose of this study was to determine the extent to which phenotypic recurrent selection for high groat-oil content influences (a) mean expression of unselected agronomic traits, (b) genetic variation for these traits, and (c) magnitude of correlation of these traits with groat-oil content and oil yield.

MATERIALS AND METHODS

Genetic Materials

Materials evaluated in this study were developed through selection procedures described in detail elsewhere (Branson, 1987). Briefly, three cycles of phenotypic recurrent selection were conducted for high groat-oil content. The base population (C_0) from which improved populations (C_1, C_2, and C_3) were derived was an introgressed oat gene pool constructed to allow recovery of enhanced genetic variation within an adapted agronomic background. Included in the present study were (a) 100 random F_1-derived lines from each of the C_0, C_1, C_2, and C_3, (b) four check varieties ('Starter', 'Webster', 'Ogle', and 'Noble') each entered five times per replication, and (c) the A. sativa and A. sterilis parents used to develop the C_0 gene pool. Random lines from C_0 through C_2 were F_1-derived in F_3 whereas those from C_3 were F_1-derived in F_2.

Evaluation Experiment

The 400 random F_1-derived lines plus parents and check varieties were grown in a randomized complete block design with two replications at each of three locations. A plot was a hill (Frey, 1965) sown with 20 seeds and hills were spaced 30.5 cm apart in perpendicular directions. Two rows of hills were sown around the experiment to reduce border effects. Plots were sown at the Agronomy Field Research Center near Ames, Iowa, the Northern Research Center near Kanawha, and the Northwestern Research Center near Sutherland, Iowa. Soil types were Clarion-Webster

loams at Ames and Kanawha and Galva-Sac silty clay loams at Sutherland. Nitrogen, phosphorus, and potassium were applied at rates of 34-22-28 kg ha^{-1} at Ames, 52-3-4 kg ha^{-1} at Kanawha, and 17-29-18 kg ha^{-1} at Sutherland prior to sowing. All plots were sprayed with a systemic fungicide (Bayleton) to control leaf diseases.

Five traits were measured or computed on a plot basis. Heading date (HD) was recorded at Ames as the number of days from seeding to 50% of plants with full panicle emergence. Plant height (HT), recorded at Kanawha, was the distance (cm) from ground level to panicle tips. When mature, each plot was harvested, dried, and weighed to obtain biomass (BM), then threshed, and grain yield (GY) was determined. Biomass and grain yield were expressed in Mg ha^{-1}. Harvest index (HI) was computed as the ratio of grain yield to biomass and expressed as a percentage.

An additional six traits were measured or computed on three replication bulks formed by combining seed of the two replications of an entry at each location. Bulking entry replications was necessary to provide sufficient seed for analysis and to keep evaluation costs minimal. Test weight (TW) was then determined as the weight of a standard volume of grain and expressed in kg m^{-3}. Seed weight (SW) was the weight (g) of 100 random seeds, and groat fraction (GF), the ratio of caryopsis weight to seed weight, was determined for a one-gram sample of manually dehulled seed expressed in g kg^{-1}. Groat yield (GTY) was computed as the product of grain yield and groat fraction and expressed in Mg ha^{-1}. To determine groat-oil content (GO), enough seeds were dehulled to give 3.5 to 5.0 g of oven-dried groats. The groat sample was evaluated for oil content

by using the nuclear magnetic resonance (NMR) method[1] described by Conway and Earle (1967) and then expressed in g kg^{-1}. Oil yield (OLY) was computed as the product of groat yield and groat-oil content and expressed in Mg ha^{-1}.

Statistical Analyses

An analysis of variance was performed for each trait using standard statistical procedures (Cochran and Cox, 1957), with cycles as fixed and environment and lines within cycles as random effects. Quasi F-tests (Satterthwaite, 1946) were used to test for cycle main effects. Fisher's protected L.S.D. test was used to compare cycle means (Steel and Torrie, 1980). Replicated check varieties in each experiment provided an estimate of experimental error for those traits measured on replication bulks.

Phenotypic (σ_p^2) and genotypic (σ_g^2) variances were estimated for each cycle of selection from the analysis of variance and broad-sense heritability was estimated as:

$$h^2 = \sigma_g^2 / \sigma_p^2$$

Standard errors of variance components and broad-sense heritability were calculated by using the methods of Anderson and Bancroft (1952) and Dickerson (1969), respectively.

Linear regression of cycle means on cycle numbers was computed for

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[1]Appreciation is expressed to Dr. D. E. Alexander and Ms. Evelyn Marriott, Agronomy Department, University of Illinois, Urbana, IL, who conducted the NMR oil analyses.

all unselected agronomic traits to determine if changes in these traits had occurred with selection for groat-oil content.

Phenotypic and genetic correlations (r) for groat-oil content and oil yield with unselected agronomic traits were calculated on an entry means basis using the formula:

$$r = \sigma_{ab} / \sqrt{\sigma_a^2 \cdot \sigma_b^2}$$

where σ_{ab} is the phenotypic or genotypic covariance between traits a and b, and σ_a^2 and σ_b^2 are the phenotypic or genotypic variances for traits a and b, respectively. Because heading date and plant height were recorded only at single locations, genetic covariances for both traits were estimated by simple covariance analysis using heading date measured at Ames and other traits measured at Kanawha, and plant height measured at Kanawha and other traits measured at Ames. Phenotypic correlations for heading date and plant height with other traits were calculated from data recorded at Ames and Kanawha, respectively.

RESULTS AND DISCUSSION

Means and Correlated Responses

Cycle means for agronomic traits are presented in Table 1. With the exception of harvest index and heading date, significant differences could not be detected between cycle means for any unselected trait (analysis of variance not shown). Harvest index differed from C_2 to C_3, an increase of two percentage points, while heading date declined approximately two days from C_0 to C_1.

Interaction of cycle means with locations, although statistically significant ($P < 0.01$) for all traits measured over locations, was considered of minor importance in this study. Changes observed in cycle mean rankings over locations were without apparent order; thus, for presentation, correlated responses to selection were averaged over locations. Selection for high groat-oil content resulted in no correlated change in mean expression of any agronomic trait. No linear regression coefficient for any trait was significant (Table 1) suggesting that either groat-oil content of oats is inherited independently of the other traits or any genetic linkages present were broken during the random mating of selected lines.

Development of the C_0 gene pool through careful parental selection and combination has resulted in the improvements in groat-oil content being made within a background suitable agronomically for cultivation in the midwestern USA. Mean grain yield, biomass, groat yield, and harvest index of the high-oil oat lines are equal or superior to those of

Table 1. Means of agronomic traits measured on random lines from C_0, C_1, C_2, C_3, populations from recurrent selection for groat-oil content, A. sativa parents, and check varieties and linear response per cycle (b), averaged over three locations

Cycle	GY	BM	GTY	TW	GF	SW	HI	HD	HT
	-------Mg ha^{-1}------			kg m^{-3}	g kg^{-1}	g	%	days	cm
C_0	3.01	7.10	2.09	388.50	691.5	2.71	42.21	77.2	82.6
C_1	3.06	7.11	2.16	387.97	701.9	2.66	43.01	75.5	82.3
C_2	3.18	7.38	2.22	380.70	696.6	2.61	42.99	76.2	82.1
C_3	3.04	6.72	2.13	382.21	699.5	2.62	45.30	76.0	82.6
FLSD (0.05)[a]	ns[d]	ns	ns	ns	ns	ns	1.24	0.9	ns
A. sativa parents	2.79	6.70	1.98	407.46	703.2	2.87	41.44	78.7	83.2
LSD (0.05)[b]	0.26	0.57	0.19	8.58	14.8	0.07	1.18	0.7	1.9
Check varieties	3.08	7.03	2.20	415.55	711.6	2.98	44.10	77.5	82.7
LSD (0.05)[c]	0.25	0.56	0.18	8.20	14.3	0.07	1.12	0.7	1.7
Linear response (b)	0.02	-0.09	0.02	-2.61	1.8	-0.03	0.93	-0.28	-0.1
Standard error	0.04	0.14	0.03	1.14	2.0	0.01	0.33	0.34	0.1

[a]Applicable to cycle mean comparisons.

[b]Applicable to comparison of cycle means and A. sativa parents.

[c]Applicable to comparison of cycle means and check varieties.

[d]ns, nonsignificant at the 0.05 probability level.

the A. sativa parents used to construct the C_0 gene pool and, with the exception of harvest index, equivalent to the mean of the check varieties (Table 1). Harvest index of C_0 was significantly less than the mean of the check varieties but C_3 was equivalent to them. Test weight and seed weight were lower than those of either the A. sativa parents or the check varieties. Improved populations matured earlier than the A. sativa parents and were similar in height to the check varieties. Early maturity, however, is a desirable characteristic in oat cultivars for the Midwest because it allows them escape from excessive heat during anthesis. Failure of the A. sterilis gene pool parents to germinate due to a seed dormancy precluded their comparisons with the improved populations.

Genetic Variances and Heritabilities

Selection for high groat-oil content caused no consistent change in genetic variance for grain yield, groat yield, biomass, or harvest index, but genetic variances for test weight and groat fraction declined 28% and 70%, respectively, over the three selection cycles (Table 2). Reductions in genetic variance from C_0 to C_1 were noted also for seed weight (30%), heading date (20%), and plant height (40%). These declines in genetic variance may result from independent culling of populations for good agronomic type rather than selection for high groat-oil content. Populations were culled, in the C_1 in particular, for plants of extremes in maturity and height and low seed weight. Indirect culling of plants with grain of low groat fraction and test weight may have occurred because samples of grain taken for groat-oil determinations were discarded

Table 2. Broad-sense heritabilities (h^2) and genetic variances (σ_g^2) for unselected traits estimated from random oat lines from the base population and three cycles of recurrent selection for groat-oil content when tested at three locations in 1986

Cycle	$h^2 \pm$ S.E.	$\sigma_g^2 \pm$ S.E.	$h^2 \pm$ S.E.	$\sigma_g^2 \pm$ S.E.	$h^2 \pm$ S.E.	$\sigma_g^2 \pm$ S.E.
	Grain yield		Test weight		Groat fraction	
		($\times 10^{-3}$)				
C_0	55.7 ± 14.8	127 ± 34	75.0 ± 14.3	513.45 ± 97.79	49.2 ± 15.0	424.56 ± 129.22
C_1	47.6 ± 15.0	78 ± 25	75.3 ± 14.3	483.54 ± 91.73	51.6 ± 14.9	359.81 ± 103.80
C_2	70.4 ± 14.4	191 ± 39	71.9 ± 14.4	392.96 ± 78.45	45.9 ± 15.1	289.01 ± 94.90
C_3	70.0 ± 14.4	159 ± 33	79.8 ± 14.2	371.85 ± 66.01	23.9 ± 16.0	125.91 ± 84.43
	Seed weight		Groat yield		Biomass	
		($\times 10^{-5}$)		($\times 10^{-5}$)		($\times 10^{-3}$)
C_0	83.3 ± 14.2	6833 ± 1162	56.7 ± 14.7	7167 ± 1860	60.5 ± 14.6	678 ± 164
C_1	78.6 ± 14.2	4767 ± 863	50.2 ± 14.9	4867 ± 1448	55.8 ± 14.8	484 ± 128
C_2	82.3 ± 14.2	5267 ± 908	65.8 ± 14.5	8833 ± 1945	69.6 ± 14.4	805 ± 166
C_3	82.2 ± 14.2	4300 ± 742	68.6 ± 14.4	8300 ± 1745	70.5 ± 14.4	721 ± 147
	Harvest index		Heading date		Height	
C_0	59.3 ± 14.7	7.87 ± 1.94	97.4 ± 14.1	12.01 ± 1.74	77.9 ± 14.1	31.12 ± 5.64
C_1	58.0 ± 14.7	4.80 ± 1.21	96.8 ± 14.1	9.74 ± 1.42	68.8 ± 14.2	19.49 ± 4.01
C_2	65.7 ± 14.5	6.74 ± 1.49	96.8 ± 14.1	9.90 ± 1.44	75.1 ± 14.1	26.58 ± 5.00
C_3	62.2 ± 14.6	4.24 ± 1.00	97.2 ± 14.1	11.18 ± 1.62	76.3 ± 14.1	28.43 ± 5.26

when difficult to dehull. If short and tall plants of early and late maturity were culled equally, changes in the genetic variance but not the population mean of both traits would be expected to occur. Such is the case for plant height but not heading date where both mean and variance declined, suggesting more late plants than early were culled from the population. Lack of significant differences between cycle means for seed weight, test weight, and groat fraction despite culling suggests an equivalent number of high performance lines may have been lost from the population. Expression of groat-oil content on a percentage basis may result in high seed weight, test weight, and groat fraction lines not being selected because of an apparent low groat-oil content.

Although genetic variance declined for several traits, broad-sense heritability estimates indicate that gains from selection are likely for all traits but groat fraction (Table 2). Broad-sense heritability is high for test weight, seed weight, heading date, and plant height and moderate for grain yield, groat yield, biomass, and harvest index. Broad-sense heritability for groat fraction declined to a low level in C_3 reflecting the change in genetic variance.

Phenotypic and Genetic Correlations

Phenotypic and genetic correlation coefficients between groat-oil content and agronomic traits were of similar sign and magnitude, indicating minor environmental influence upon trait associations (Table 3). Although small in magnitude and often not significant, negative relationships between groat-oil content and several traits are apparent.

Table 3. Phenotypic and genetic (lower value) correlations for groat-oil content with other traits averaged over three locations

Trait	C_0	C_1	C_2	C_3
Grain yield	-0.02	-0.12	0.01	-0.18
	-0.05	-0.22	-0.02	-0.24
Test weight	-0.16	-0.26**	-0.09	-0.37**
	-0.17	-0.29	-0.10	-0.40
Groat fraction	-0.18	-0.16	-0.22*	-0.12
	-0.24	-0.22	-0.33	-0.16
Seed weight	-0.20*	-0.24*	-0.22*	-0.31**
	-0.22	-0.27	-0.25	-0.32
Groat yield	-0.06	-0.15	-0.04	-0.19
	-0.09	-0.24	-0.07	-0.25
Biomass	-0.12	-0.08	-0.06	-0.10
	-0.17	-0.13	-0.08	-0.13
Harvest index	0.17	-0.12	0.16	-0.24*
	0.19	-0.19	0.17	-0.34
Heading date	-0.08	-0.11	0.11	0.19
	-0.10	-0.18	0.05	0.15
Plant height	0.07	-0.20*	0.01	0.21*
	0.02	0.19	0.01	0.11

*,**Significant at the 0.01 and 0.05 probability levels, respectively.

Groat-oil content was negatively correlated with seed weight and the correlation was significant across all selection cycles. Previously, groat-oil content and seed weight have been reported to be either independent (Brown et al., 1966; Baker and McKenzie, 1972; Gullord, 1980) or positively associated (Forsberg et al., 1974). Grain yield and groat-oil content were negatively associated in this study but the correlations were not significant. However, in the studies of Gullord (1980) and Thro and Frey (1984), significant positive correlation between grain yield and groat-oil content were obtained. Correlations of groat-oil content with test weight, groat fraction, groat yield, and biomass were consistently negative across selection cycles though rarely reaching a level of statistical significance. Groat-oil content had no association with heading date and only minor associations with harvest index and plant height.

Such negative relationships between traits may reflect a bioenergetic limitation to increasing groat-oil content. Following a survey of biochemical pathways in plants and their energy requirements, Penning de Vries et al. (1974) concluded that, under aerobic conditions, 1 gram of glucose would be used to produce 0.83 gram of carbohydrates, 0.40 gram of protein, or 0.33 gram of lipids. Obviously, the glucose requirement for oil synthesis is greater than for either carbohydrates or protein. Thus, with a fixed rate of photosynthate production, it follows that increases in the oil content of a grain should reduce both protein percentage and yield. Mitra and Bhatia (1979) calculated the bioenergetic cost of increasing oil content in peanut (Arachis hypogaea L.) to be

least when accompanied by a reduction in protein percentage. Increasing oil content at the cost of carbohydrates is bioenergetically the most expensive. Following Mitra and Bhatia (1979), the production value of oat oil was calculated to be 0.2982 from which it can be shown (C. Branson, Department of Agronomy, Iowa State University, Ames, Iowa, unpublished data) that the increase in groat-oil content obtained by Branson (1987) from the C_0 mean of 84.96 g kg^{-1} to the C_3 mean of 113.30 g kg^{-1} would require an additional 95.1 g glucose. Further, if all additional glucose was derived from foregone carbohydrate synthesis, significant decreases in seed weight would result. Failure to detect such a change suggests that at least some glucose was derived from foregone synthesis of proteins.

Selection for high groat-oil content in oats is in itself not useful unless those increases result in higher oil production per unit area. Branson (1987) has shown that improvements in oil yield do result from increases in groat-oil content. Phenotypic and genetic correlation coefficients for oil yield with agronomic traits suggest that the increases obtained in oil yield were due, in part, to increases in grain and groat yields (Table 4). Oil yield is highly correlated with both grain and groat yield, moderately correlated with groat fraction, biomass, and harvest index, and has low correlation with seed weight, heading date and plant height. Takeda and Frey (1976) have shown that from 92 to 97% of the variation in grain yield for progenies of A. sativa x A. sterilis crosses was due to variation in harvest index and vegetative growth rate, so biomass and harvest index may influence oil yield indirectly through

Table 4. Phenotypic and genetic (lower value) correlations for oil yield with other traits averaged over three locations

Trait	C_0	C_1	C_2	C_3
Grain yield	0.80**	0.77**	0.88**	0.87**
	0.72	0.65	0.86	0.85
Test weight	0.08	0.07	-0.01	0.14
	0.01	-0.07	-0.13	0.19
Groat fraction	0.27**	0.31**	-0.03	0.25**
	0.24	0.28	-0.31	0.29
Seed weight	-0.09	-0.28**	-0.02	-0.03
	-0.24	-0.46	-0.06	-0.04
Groat yield	0.80**	0.79**	0.87**	0.88**
	0.72	0.64	0.84	0.35
Biomass	0.62**	0.69**	0.77**	0.84**
	0.53	0.59	0.77	0.84
Harvest index	0.42**	0.23*	0.47**	0.20*
	0.37	0.07	0.47	0.14
Heading date	-0.08	0.13	0.18	0.18
	-0.22	-0.01	0.01	0.15
Plant height	0.17	0.31**	0.19	0.40**
	0.20	0.28	0.24	0.31

*,**Significant at the 0.01 and 0.05 probability levels, respectively.

their effect upon grain yield.

Development of oilseed oat cultivars will require a substantial increase in groat-oil content over that which is presently available. Frey and Hammond (1975) estimate an oat combining 170 g kg^{-1} groat-oil content with current levels of groat-protein and grain yield would compete economically with soybeans (Glycine max (L.) Merr.) as a source of edible vegetable oil. Results of this study demonstrate that the increase in groat-oil content and indirectly oil yield obtained by Branson (1987) has been made without significant changes occurring in unselected agronomic traits. Phenotypic recurrent selection for groat-oil content is an effective means of increasing oil yield; however, multiple trait selection incorporating groat-oil content, groat or grain yield, and protein percentage may result in greater oil yield gains being made particularly if bioenergetic limitations to increased groat-oil content become important.

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GENERAL CONCLUSIONS

The results of this study have important implications for (a) the genetic improvement of groat-oil content in oats, (b) the application of recurrent selection breeding techniques to self-fertilizing species, and (c) the use of germplasm from wild relatives for crop improvement.

Previous research suggests that given the correct breeding procedure, a genetic improvement in the groat-oil content of oats and the subsequent development of oilseed oat cultivars is likely. Groat-oil content is maternally inherited (Brown and Aryeetey, 1973), is under polygenic control with largely additive gene action (Brown et al., 1974), has high character heritability (Stuke, 1960), and low genotype x environment interaction (Baker and McKenzie, 1972). Also, genetic variation for groat-oil content exists within cultivated and wild oat species (Brown and Craddock, 1972; Rezai, 1977). Further, correlations between groat-oil content and other production associated traits are often small and nonsignificant which suggests that groat-oil content can be manipulated independently of those traits.

Results of the present study support previously published findings and demonstrate that a substantial genetic improvement in groat-oil content can be rapidly made without any correlated changes in mean expression of unselected agronomic traits. In Section I of this study, groat-oil content of oats was increased 9.26 g kg^{-1} in each of three selection cycles with a concomitant increase in oil yield of 21 kg ha^{-1} per cycle. Genetic variance for groat-oil content declined with

continued selection but broad-sense heritability remained high, suggesting further gains are likely. Phenotypic recurrent selection has resulted in C_3 lines superior to the best C_0 lines and with more than double the groat-oil content and oil yield of current commercial oat cultivars; thus, this procedure is an effective breeding procedure for the development of oilseed oat cultivars. Section II of this study demonstrated selection for high groat-oil content caused no significant correlated changes in mean expression of unselected agronomic traits. Changes in genetic variance did occur for several traits and may have resulted either from selection for high groat-oil content or independent culling for good agronomic type. Negative trends in correlation coefficients between groat-oil content and several traits, although not significant, may indicate a bioenergetic limitation to the increase of oil content of oats.

Recurrent selection techniques have proven useful for the genetic improvement of quantitatively inherited traits in cross-fertilizing crop species (Hallauer, 1985); however, their application to the improvement of such traits in self-fertilizing crop species has been limited. In the past, difficulties have arisen in recombining selected lines and getting sufficient progeny seed for evaluation. The common belief among plant breeders that early generation evaluation is ineffective has led to the practice of evaluating highly inbred lines, which consequently, lengthens cycle time. Results of this study (Section I) demonstrate that the difficulties in recombining selected lines can easily be overcome in oats by using an approach crossing system and that early

generation evaluation of groat-oil content is effective. Nuclear magnetic resonance oil analysis proved a rapid and accurate method of determining groat-oil content and together with the use of greenhouse facilities allowed for the completion of one selection cycle per year.

Finally, introgression of genes from wild and weedy relatives of crop species into cultivated gene pools can enhance genetic variance for a particular trait but may result in a concomitant decline in mean performance of other production associated traits due, in part, to either linkage drag or residue of random genes that condition unadaptiveness. Development of the C_0 gene pool used in this study (Section I) is an example of how, through careful parental selection and combination, genes from wild and cultivated species can be combined into an agronomically adapted population suitable for use in recurrent selection.

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APPENDIX

Table A1. Abbreviation of traits presented in Appendix tables

Abbreviation	Trait	Units
GO	Groat-oil content	Mg ha^{-1}
TW	Test weight	kg m^{-3}
GF	Groat fraction	g kg^{-1}
SW	Seed weight	g
GTY	Groat yield	Mg ha^{-1}
OLY	Oil yield	Mg ha^{-1}
GY	Grain yield	Mg ha^{-1}
BM	Biomass	Mg ha^{-1}
HI	Harvest index	%
HD	Heading date	days
HT	Plant height	cm

Table A2. Analysis of variance, degrees of freedom, and expected mean squares for traits evaluated from bulk seed lots representing both entry replications per location, analyzed in a randomized complete block design

Source of variation	df	EMS[a]
Environment(E)	e-1	$\sigma_e^2 + rLC\sigma_E^2$
Cycle (C)	c-1	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rE\sigma_{L(C)}^2 + rL\sigma_{EC}^2 + rELk_1^2$
E x C	(e-1)(c-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rL\sigma_{EC}^2$
Line (C)	c(l-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rE\sigma_{L(C)}^2$
E x line (C)	c(e-1)(l-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2$
Error[b]	e(r-1)(g-1)	σ_e^2

[a] k_1^2 represents a fixed effect.

[b] Error term obtained from four check varieties (g) replicated five times per environment.

Table A3. Analysis of variance, degrees of freedom, and expected mean squares for traits evaluated in a randomized complete block design at one location

Source of variation	df	EMS[a]
Replication	r-1	$\sigma_e^2 + LC\sigma_r^2$
Cycle (C)	c-1	$\sigma_e^2 + r\sigma_{L(C)}^2 + rLk_1^2$
Line (C)	c(l-1)	$\sigma_e^2 + r\sigma_{L(C)}^2$
Error	(r-1)(cl-1)	σ_e^2

[a] k_1^2 represents a fixed effect.

Table A4. Analysis of variance, degrees of freedom, and expected mean squares for traits evaluated in a randomized complete block design at three locations

Source of variation	df	EMS[a]
Environment (E)	e-1	$\sigma_e^2 + LC\sigma_{r(E)}^2 + rLC\sigma_E^2$
Replication	e(r-1)	$\sigma_e^2 + LC\sigma_{r(E)}^2$
Cycle (C)	c-1	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rE\sigma_{L(C)}^2 + rL\sigma_{EC}^2 + rEk_1^2$
E x C	(e-1)(c-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rL\sigma_{EC}^2$
Line (C)	c(1-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2 + rE\sigma_{L(C)}^2$
E x line (C)	c(e-1)(1-1)	$\sigma_e^2 + r\sigma_{EL(C)}^2$
Error	e(r-1)(c1-1)	σ_e^2

[a] k_1^2 represents a fixed effect.

Table A5. Analysis of variance, means, and coefficients of variation (CV) for traits evaluated from bulk seed lots representing all replicates at three environments

Source	df	Trait					
		GO	TW	GF	SW	GTY	OLY
					($\times 10^{-3}$)	($\times 10^{-3}$)	($\times 10^{-5}$)
Environment (E)	2	23423.53**	1896415.03**	102597.95**	31259**	305344**	245893**
Cycle (C)	7	34073.06**	9137.02**	7433.54	872**	2043	18989**
Random (R)/C	3	44166.34**	4722.64	5591.91	572	896	24915**
C Lin	1	128758.67**	10247.40	4581.16	1369	489	68395*
C Quad	1	3287.89	314.76	3755.94	285	1856	6250
Residual	1	452.45	3605.77	8438.63	64	345	103
Selected (S)/C	3	32979.79**	11747.84	10184.60	1383	755	18592*
C Lin	1	80784.42	9406.88	24745.58	3642	1781	50639
C Quad	1	13539.65	10380.42	5659.77	335	16	4755
Residual	1	4615.31	15456.22	148.45	171	466	384
R/C vs S/C	1	7073.05**	14547.69**	4705.23	237	9351*	2398
E x C	14	118.99**	1313.16**	9567.13**	76**	1603**	1477**
E x random/C	6	115.89**	1167.91**	2792.37**	49**	2391**	1468**
E x C Lin	2	301.79**	2097.64**	2950.01**	104*	6240**	2990**
E x C Quad	2	25.77	1123.13	5156.26**	14	210	548
E x Residual	2	20.09	282.96	270.83	31	725**	869**
E x selected/C	6	85.88**	1775.23**	18715.62**	126**	975**	1264**
E x C Lin	2	157.08**	1611.08*	11420.46**	70	1367**	1006**
E x C Quad	2	70.62*	2708.61**	25376.29**	178**	1285**	2355**
E x Residual	2	29.94	1005.99	19350.11**	132**	273	432
E x R/C vs S/C	2	227.60**	362.70	2445.91	4	1125**	2142*
Lines/C	707	271.67*	1913.95**	1933.29**	200**	305**	387**
Random	396	296.52**	1753.02**	2038.79**	194**	358**	463**

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table A5. (Continued)

Source	df	Trait					
		GO	TW	GF	SW	GTY	OLY
					(x 10^{-3})	(x 10^{-3})	(x 10^{-5})
C0	99	351.56**	2052.67**	2590.99**	246**	379**	387**
C1	99	312.42**	1926.14**	2092.58**	182**	291**	366**
C2	99	262.20**	1640.02**	1888.55**	192**	403**	582**
C3	99	259.90**	1393.28**	1583.06*	157**	363**	520**
Selected	311	240.04**	2118.86**	1798.94**	208**	238**	290**
Parents	14	417.42**	780.37**	3468.28**	268**	445**	430**
C0	99	343.66**	3039.00**	2427.09**	267**	272**	294**
C1	99	183.27**	1896.76**	1329.40**	183**	209*	258**
C2	99	168.11**	1610.12**	1404.27**	168**	204*	300**
E x lines/C	1414	28.62	452.88	1169.96	35	139	158**
E x R/C	792	26.98	431.68	1139.33	35	140	151**
E x S/C	622	30.71	479.89	1208.96	36	138	167**
Error[a]	36	20.47	384.33	913.11	23	113	31
Expt. Mean		102.40	382.53	696.16	2.64	2.09	0.21
Expt. CV (%)		5.22	5.56	4.91	7.09	17.84	16.93

[a]Error term obtained from four check varieties replicated five times per environment.

Table A6. Analysis of variance, means, and coefficients of variation (CV) for traits evaluated in two replications at three environments

Source	df	Mean square		
		GY	BM	HI
Environment (E)	2	1127.57**	5739.03**	842.83
Replication/E	3	2.96**	28.42**	381.91**
Cycle (C)	7	7.39	39.18	620.87**
Random (R)/C	3	3.17	44.50	1069.18**
C Lin	1	1.10	23.58	2566.30**
C Quad	1	5.07	67.53	343.69
Residual	1	3.33	42.39	297.54
Selected (S)/C	3	2.12	10.75	202.03*
C Lin	1	2.84	0.36	505.49*
C Quad	1	0.19	3.32	32.70
Residual	1	3.35	28.58	67.90
R/C vs S/C	1	35.88*	108.52	532.45**
E x C	14	7.01**	33.65**	59.00**
E x random/C	6	11.15**	53.89**	80.59**
E x C Lin	2	29.66**	149.39**	125.84**
E x C Quad	2	0.52	0.89	54.47
E x Residual	2	3.27**	11.39**	61.47
E x selected/C	6	3.80**	18.86**	27.93
E x C Lin	2	8.78**	46.69**	67.85
E x C Quad	2	2.56**	9.51*	15.16
E x Residual	2	0.06	0.37	0.79
E x R/C vs S/C	2	4.24**	17.32**	87.39*
Lines/C	707	1.13**	5.46**	57.28**
Random	396	1.34**	6.24**	57.96**
C0	99	1.37**	6.72**	79.65**
C1	99	0.99**	5.20**	49.58**
C2	99	1.63**	6.91**	61.64**
C3	99	1.36**	6.13**	40.98**
Selected	311	0.85**	4.47**	56.41**
Parents	14	1.29**	5.54**	51.10**
C0	99	1.01**	5.87**	83.14**
C1	99	0.78**	4.21**	47.77**
C2	99	0.71**	3.18*	39.09**

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table A6. (Continued)

Source	df	Mean square		
		GY	BM	HI
E x Lines/C	1414	0.50**	2.23**	22.64**
E x R/C	792	0.50**	2.21**	22.48**
E x S/C	622	0.49**	2.26**	22.84**
Error	2142	0.40	1.93	15.95
Expt. mean		2.99	6.94	43.07
Expt. CV (%)		21.12	20.03	9.27

Table A7. Analysis of variance, means, and coefficients of variation (CV) for traits evaluated in two replications at one environment

Source	df	Mean square HD	Mean square HT
Replication	1	0.55	3187.57**
Cycle (C)	7	71.63**	334.84
Random (R)/C	3	102.53**	11.52
C Lin	1	77.56	0.17
C Quad	1	114.76*	29.64
Residual	1	115.26*	4.76
Selected (S)/C	3	59.13*	85.04
C Lin	1	144.41*	41.76
C Quad	1	32.56	159.07
Residual	1	0.42	54.31
R vs S	1	16.43	45.14
Lines/C	707	22.06**	69.14**
Random	396	22.06**	70.44**
C0	99	24.68**	79.88**
C1	99	20.13**	56.61**
C2	99	20.44**	70.79**
C3	99	23.01**	74.49**
Selected	311	22.06**	67.48**
Parents	14	22.35**	136.51**
C0	99	24.14**	71.53**
C1	99	18.50**	54.01**
C2	99	23.49**	67.12**
Error	714	0.65	17.63
Expt. mean		76.35	82.28
Expt. CV (%)		1.05	5.10

*,**Significant at the 0.05 and 0.01 probability levels, respectively.